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Shading and sediment structure effects on stream metabolism resistance and resilience to infrequent droughts

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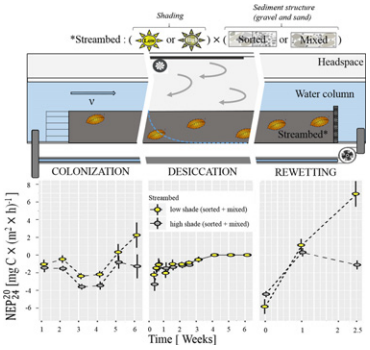
HIGHLIGHTS

- Shading affects stream metabolism (NEP, CR) resistance and resilience to infrequent droughts.
- Transition to microbial community during drying is shaped by sediment structures.
- Periphyton has capacity to adapt to drying only when light exceeds given threshold.
- The microbial community shifts during drying and rewetting result in decoupled NEP and CR.
- Stream management is key to mitigate future infrequent intermittency under changing climate and land use.

GRAPHICAL ABSTRACT



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ABSTRACT

Perennial, temperate, low-order streams are predicted to become intermittent as a result of irregular droughts caused by global warming and increased water demand. We hypothesize that stream metabolism changes caused by irregular droughts are linked to the shading and bed sediment structure of temperate streams. We set up 16 outdoor experimental streams with low or high shade conditions and streambeds either with alternating sorted patches of gravel and sand or homogeneous gravel-sand mix sediment structures. We assessed community respiration (CR), net ecosystem production (NEP) and periphyton biomass and structure (diatoms, green algae, cyanobacteria) in the course of 6 weeks colonization, 6 weeks desiccation, and 2.5 weeks after rewetting. The heterotroph to autotroph (H:A) and fungi to bacteria (F:B) ratios in the microbial biofilm community were assessed at the end of the colonization and rewetting phases. Streams with different bed sediment structure were functionally similar; their metabolism under desiccation was controlled solely by light availability. During flow recession, all streams showed net heterotrophy. As desiccation progressed, NEP and CR decreased to zero. Desiccation altered the periphyton composition from predominantly diatoms to green algae and cyanobacteria, particularly in streams with low shade and mixed sediments. Rapid post-drought resilience of NEP was accompanied by high cyanobacteria and green algae growth in low shade, but poor total periphyton growth in high shade streams. Variable periphyton recovery was followed by increased H:A in relation to shading, and decreased F:B in relation to sediments structure. These shifts resulted in poor CR recovery compared to the colonization phase, suggesting a link between CR resilience and microbial composition changes. The links between

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drought effects, post-drought recovery, shading level, and streambed structure reveal the importance of low-order stream management under a changing climate and land use to mitigate the future impact of unpredictable infrequent droughts on stream metabolism in temperate ecosystems.

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1. Introduction

Intermittent streams and rivers, watercourses that cease to flow at some points in time and space, represent 69% of global first-order streams below 60° latitude (Raymond et al., 2013). Most predictions agree that the combined effects of irregular climate patterns (Botter et al., 2013; Reynolds et al., 2015) and increasing water abstraction (Barceló and Sabater, 2010; Larned et al., 2010) will cause a shift in many temperate low-order streams from permanent to intermittent flow regimes, with infrequent and brief zero-flow periods and stream bed desiccation (Datry et al., 2017; Krysanova et al., 2010). Hence, unpredictable desiccation will challenge microbial communities and ecosystem functions in temperate streams (Bogan et al., 2015; Lake, 2003).

Desiccation and rewetting are increasingly recognized as major stressors of streams ecosystems (Sabater et al., 2016). Species richness and diversity decline significantly in most biofilm microbial communities during prolonged dry periods (Acuna et al., 2015; Pohlon et al., 2013; Rothrock and Garcia-Pichel, 2005). Flow resumption in previously dried streambeds causes rewetting that adds additional stress to the sediment community (Romaní and Sabater, 1997). Studies of laboratory microcosms with disturbed hyporheic sediments indicate that more intense drying results in more distinct changes and reduction in the microbial community (Marxsen et al., 2010). In streams impacted by desiccation, algal communities react quickly after flow cessation, while heterotrophs take longer to react (Acuna et al., 2015). Given the disparate reactions of communities to drying, autotrophic and heterotrophic dominated ecosystems controlled by the light availability may respond differently to drying stress affecting stream metabolism and its recovery after flow resumption (Timoner et al., 2012).

Impact of drying intensity in a natural streambed is related to sediment structure (Shokri et al., 2010). Natural streambeds are composed of textural patches (grain-size facies) (Buffington and Montgomery, 1999a; Buffington and Montgomery, 1999b) of variable sediment grain size and hydraulic conductivity (Malard et al., 2002). Such heterogeneous sediment structures support solute supply to sediment associated biofilms (Salehin et al., 2004), and provide metabolic functions (Battin et al., 2003). However, during desiccation, coarser sediment patches become sites of higher initial evaporation rates (Shokri et al., 2010), potentially increasing the impact of drying on benthic communities in sorted coarse bed sediments. In contrast, bed hydraulic conductivity is limited in hydromorphologically degraded streams. The uniformly mixed bed sediments impacted by sand from catchment erosion (Meyer et al., 2008; Wagner et al., 2015), restrict solute supply and, during drought, limit evaporation rates from deeper sediments. Opposing roles of sediment structure on microbial communities and their functions during flow and non-flow periods may have a critical impact on intermittent stream metabolism.

Although it is assumed that drought stress interacts with light availability and bed sediment structure, the response of microbial communities and functions to droughts in the complex environment of canopied temperate streams with variable bed sediment structure and shading remains unclear. We examined the functional dynamics of autotrophic and heterotrophic ecosystem metabolism during drying and subsequent rewetting in streams. We focused on the interactions of light availability (shading level) and sediment structure with stream metabolism resistance and resilience to desiccation and rewetting. While definitions vary (Allison and Martiny, 2008; Pimm, 1984; Shade et al., 2012), we define resistance as the ability of communities to withstand drying, and resilience as the capacity of communities exposed to drying and rewetting to recover rapidly, and revert to pre-drying ecosystem functions (Acuna et al., 2015; Todman et al., 2016). The hypothesis of this study was that shifts of stream ecosystem functions caused by infrequent and unpredictable droughts interact with the shading and sediment structure of temperate streams. We tested this hypothesis by analyzing 16 experimental streams, varying the light availability and bed sediment structure, and assessing microbial ratios (H:A, F:B), periphyton biomass and structure (diatoms, green algae, cyanobacteria), community respiration (CR), and net ecosystem production (NEP).

2. Material and methods

2.1. Experimental set-up

We designed a 2×2 factorial experiment comprising 16 outdoor experimental streams, using flumes ($400 \times 12 \times 8$ cm) which were filled with a 3 cm layer of sediment (Fig. 1). Two streambed structures (both with 30% porosity) were generated through different arrangements of gravel (2–10 mm grain size, d50 = 4.75 mm) and sand (0.2–2 mm grain size, d50 = 0.57 mm), rinsed with 10% hydrochloric acid and washed with groundwater prior to use. A natural streambed (sorted structure) was created by arranging eight alternating patches of gravel and sand, each 45 cm in length, in eight streams. A hydromorphologically degraded streambed (mixed structure) was created by homogenously mixing sand and gravel (50:50 vol%), which was evenly distributed in the other eight streams. In all streams, 31.25 g C m^{-2} of beech litter was homogeneously distributed in the bed sediments as a source of organic carbon to simulate the leaves deposited in natural streams during spring and summer (Romaní et al., 2013). Additionally, two shade conditions were generated. Low shade was achieved by placing a white, water-resistant polyethylene tent (180 g m^{-2}) above the streams, which reduced ambient light by 25%. High shade was achieved by also placing black net (mesh size 1.2 mm) 10 cm above half of the streams, resulting in a 55% further reduction in light. The combination of both factors, streambed structure and shading, resulted in four different experimental treatments, each in replicates of four: 1) High shade sorted, 2) Low shade sorted, 3) High shade mixed, and 4) Low shade mixed.

The experiment involved 6 weeks of initial colonization, 6 weeks of desiccation, and 2.5 weeks of rewetting. 20 L of water from a local groundwater well (+1.0 mg L^{-1} N-NO_3^-, +0.2 mg L^{-1} P-PO_4^{3-}, +0.3 mL L^{-1} SL10, Lehman, 1980) were added to each stream. Streams were operated as individual recirculation systems (pumps by EHEIM GmbH & Co. KG, Germany) with a constant mean water velocity of 2.54 ± 0.03 cm/s and a water depth of 2.8 ± 0.2 cm. Water evaporation during colonization and rewetting under ambient temperature was compensated for by adding deionized water whenever the water level decreased >0.5 cm below the initial level. Dissolved nitrogen ($NaNO_3$) and phosphorus ($K_2HPO_4 \cdot 3H_2O$) were added to the water column to maintain nutrient concentrations at a molar ratio of 20:1 whenever depletion was observed due to microbial growth. Concentrations of total organic carbon (TOC), dissolved inorganic nitrogen (DIN), and soluble reactive phosphorus (SRP) were monitored weekly during the colonization and rewetting phase.

Streams were inoculated with a microbial community isolated from the groundwater-fed Waldbach stream, Germany (52°16′N and 14°03′E), a temperate, perennial, first-order stream (average annual precipitation: 576 mm), which last experienced drought in 2003 (Bréda et al., 2006). The stream runs through deciduous forest and is fully canopied

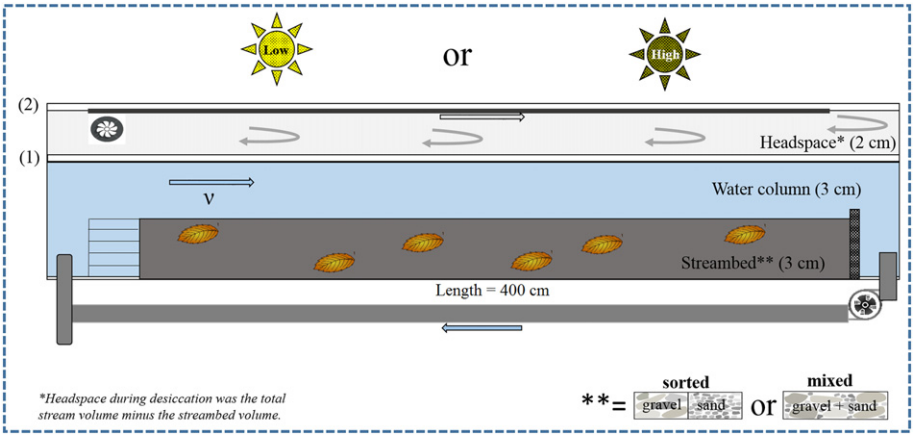

Fig. 1. Longitudinal section of the experimental stream (n = 16). Eight streams were filled with a 1:1 mix of gravel and sand (mixed) and eight streams were filled with alternating 45-cm long patches of gravel and sand (sorted). Leaves were homogeneously mixed in the sediments. Water was recirculated by pumps and pipes outside of the streams. Four streams of each substrate treatment were exposed to low shade and high shade. Streams were open to the atmosphere except during metabolism measurements when streams were covered by airtight acrylic glass lids that were lowered over the water surface without headspace during colonization and rewetting (1), or fixed to the top of experimental streams allowing headspace above the bed during desiccation (2). For measurements during desiccation, a fan attached to the lid ensured complete mixing of the headspace prior to gas sampling.

by beech (*Fagus sylvatica* L.) and alder (*Alnus glutinosa* L.). Its streambed is composed mostly of coarse sand and fine to medium gravel, and is occasionally scattered with rocks. The inoculum was generated from 16 randomly collected 500 mL sediment samples, which included litter and woody particles. Sediment samples were homogeneously mixed and incubated in 8 L of well aerated stream water for 48 h under ambient conditions. Each stream received 500 mL of inoculum suspension, previously screened through a 125 μm mesh to exclude macroinvertebrates and larger organic particles. Colonization of the streams lasted 6 weeks, followed by desiccation and rewetting (Fig. 2). The streams were open to the atmosphere and exposed to ambient temperature and atmospheric humidity between May and September, with the exception of incubation periods for O_2 and CO_2 dynamic measurement. Light intensity and water temperature were measured every 10 min by sensors deployed in each stream (ONSET HOBO Pendant® Temperature/Light 64 K Data Logger).

2.2. Stream metabolism measurements

We assessed stream metabolism on a weekly basis using day and night dissolved O_2 concentrations during the colonization and rewetting phases. Dissolved O_2 was measured in the water column with multichannel fiber oxygen optodes (Oxy 10 mini; Presens, Regensburg, Germany) at 30 min intervals over a 24 h period. During measurement, we inhibited gas exchange with the atmosphere by sealing each stream from the atmosphere with acrylic glass lids. During the desiccation phase, we assessed stream metabolism by monitoring headspace CO_2 dynamics with a gas analyzer (CCIA, Los Gatos Research, CA, USA). Streams were sealed against the atmosphere with acrylic lids on Neoprene foam (Zellpren) along the edges of the experimental stream and further with silane-terminated polymer adhesive (Terosan, Henkel, Germany) on all connections, allowing <4% of air intrusion during the 24 h period. A small tube (0.7 mm diameter), open to the atmosphere and situated on the opposite side of the headspace sampling, prevented pressure reductions while sampling.

Gas from the headspace above the sediment was pumped (650 mL min^{-1}) through a 5 m gas-tight tube for 3 min and automatically measured (10-universal multiport selectors, Vici Valco, Houston, TX, USA) every 3 h over 24 h in each experimental stream. Previous tests revealed that gas diffusion from one side of the stream to the other occurs within 50 min. Therefore, a mini fan (ACT-RX Technology Corporation, Taiwan, air flow capacity 116 L min^{-1}) was installed on the inside of the acryl lid that recirculated the headspace to ensure good mixing prior to gas sampling. The selector-analyzer network was flushed with outside air between each measurement. Before each measurement campaign, we ran a reference gas (0.15% CO_2 in 70% N_2 + 30% O_2, Airliquide, Germany) to correct for instrument concentration drifting, yielding a precision of 1 ppm for CO_2 concentration.

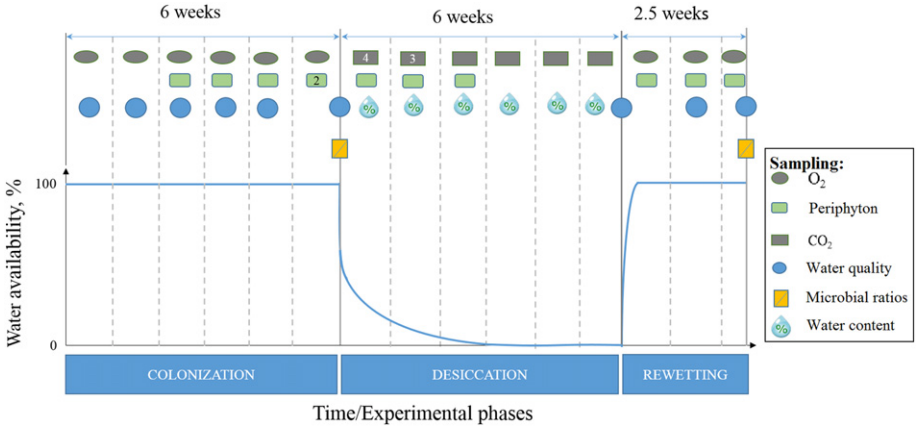

Fig. 2. Timeline of the experiment. Blue line represents the water availability in the streams during the three experimental phases. Vertical dotted lines indicate weeks. Numbers within symbols represent the number of samplings each week.

Changes in O_2 and CO_2 were converted to metabolic rates according to the following equations:

$$CR_{24} = \left(\frac{dC_{treatment}}{dt}\right)_{night} \times \left(\frac{V_{water}}{A_{sed}}\right)$$

$$NEP_{24} = \left(\frac{dC_{treatment}}{dt}\right)_{day} \times \left(\frac{V_{water}}{A_{sed}}\right) - CR_{24}$$

where $C_{treatment}$ is oxygen (mg L^{-1}) or carbon dioxide concentration (ppm), t is time (h), *night* and *day* represent the dissolved O_2 and CO_2 concentration data set used during nighttime (between 10 pm and 4 am, sunset and sunrise, respectively) and daytime (between 4 am and 10 pm) incubation, V_{water} is the total water volume (L) in the experimental streams, and A_{sed} is the stream bed surface (m^2). The rates were expressed as carbon equivalents using a respiratory quotient of 0.85 (Del Giorgio and Peters, 1994) and standardized to 20 °C using a temperature coefficient Q_{10} of 2. Both CR_{24}^{20} and NEP_{24}^{20} were expressed as daily values.

2.3. Periphyton biomass and structure

We monitored periphyton biomass and structure at eight sites in each experimental stream each week throughout the experiment using an in vivo fluorometer (Bentho Torch, bbe-Moldaenke, Germany). The Bentho Torch quantified total algal biomass via chlorophyll *a* content, and differentiated between cyanobacteria, green algae, and diatoms based on pigment fluorescence. The method allowed repeat measurements and avoided extensive sediment disturbance that would have altered drying by creating large voids. The relative proportion of cyanobacteria, green algae, and diatoms in the total algal biomass was further validated by microbial biomarkers (PLFA) specific to the three algal types from sediment samples collected at the end of colonization and rewetting phases. To avoid interference of ambient light with the instrument light beam and prevent disruption of the upper sediments, the Bentho Torch was positioned 1–2 mm above the sediment by a carrier that allowed sliding of the instrument along the stream channel. Near-bed hydraulic disturbance of the sediment by the Bentho Torch was avoided by stopping the flow during measurement (15 min).

2.4. Microbial ratios in the benthic community

After the 6 week colonization phase, and at the end of the experiment, the uppermost benthic sediments were sampled randomly using a laboratory spoon, and immediately stored at −20 °C until further processing. Microbial ratios of the sediment microbial community (heterotroph to autotroph, H:A, and fungi to bacteria, F:B) were obtained by analyzing phospholipid fatty acids (PLFAs) (Frostegard et al., 1991; Steger et al., 2011) extracted from 60 to 70 g of lyophilized sediment. PLFAs are present in the membranes of all living cells and rapidly degrade to neutral lipids upon cell death (Willers et al., 2015); hence, the method allows for sensitive and reproducible measurements characterizing viable microbial communities (Boschker and Middelburg, 2002; Weise et al., 2016). After extraction, PLFAs were separated from other lipids on silicic acid columns (BondElut®LRC-Si, Altmann Analytic, Germany) using solid-phase extraction, and methylated using mild alkaline methanolysis. The resulting fatty acid methyl esters were quantified on a GC-IRMS system (Agilent 6890, Agilent 5973, Germany). The Bayesian mixed model (FASTAR) (Galloway et al., 2014; Strandberg et al., 2015) was used to calculate the relative occurrence of autotrophs, fungi, and heterotrophic bacteria from biofilm communities obtained from the PLFA sample profiles. H:A and F:B ratios were calculated by relating the occurrence of heterotrophs to autotrophs and fungi to bacteria, respectively, in the total community biomass.

2.5. Water quality parameters

Weekly sampled water was analyzed for soluble reactive phosphorus (SRP), dissolved inorganic nitrogen (DIN: $NO_3^- + NO_2^- + NH_4^+$), and total organic carbon (TOC). Water samples for SRP and DIN were pre-filtered (Cellulose Acetate, 0.45 μm, Whatman, Germany) to remove all particles. SRP was analyzed photometrically with a UV/VIS-Photometer CARY 1E (VARIAN, Darmstadt, Germany) following a standard method (DIN EN ISO 11732) (Murphy and Riley, 1962). DIN was measured with a CFA-Photometer Skalar SAN (Skalar Analytical B.V., Breda, The Netherlands) according to DIN EN 1189. TOC was analyzed with a TOC autosampler (TOC-L CPN, Shimadzu, Japan).

2.6. Sediment hydraulic characteristics, drying, and rewetting

We measured vertical water flux (VWF) between the water column and the sediment at the beginning of the colonization phase to determine the hydraulic properties of the streambed. We added uranine to the water column of each experimental stream (3 μg L^{-1} final concentration). Surface water was uniformly colored with uranine after 15 min (based on previous tests). A field fluorometer (LLF-M Fiber-Optic fluorometer; Gotschy Optotechnik, Adnet, Austria) measured the decrease in uranine concentrations by measuring the exchange of colored surface water with uncolored water from the sediment pore space, allowing calculation of the vertical water exchange (Mutz et al., 2007). Before desiccation, surface and free sediment pore water were drained from the experimental streams by elevating one side of the stream by 5 cm for 30 min, after which the streams were returned to their horizontal position. The remaining water was evaporated from the moist sediment under ambient temperature and humidity in July and August.

We measured the pore water loss during desiccation in two additional streams, one for each sediment structure, that were weighed daily, and then calculated the gravimetrical water content. When no difference in weight was observed by weighing entire streams, transects of moist sediments were sampled instead, dried at 105 °C for 48 h, and the gravimetric water content was calculated. Streams were rewetted by simulating a heavy rain shower (23 mm) on the dry streambed. Low nutrient groundwater was sprayed from watering cans for 20 min on the streambed, taking care not to destroy the sediment surface. After pores were filled and the bed was covered by a thin film of water, we stopped rewetting to simulate a short period (3 h) without strong surface flow, as observed in streams rewetted by rain in nature (Datry et al., 2014). Then, the water column was filled to a defined depth, and flow was restored.

2.7. Statistical analysis

We applied a linear mixed-effects (LME) model to relate the observed differences in stream metabolic function (CR, NEP) and periphyton between experimental phases (colonization, desiccation, and rewetting) to levels of shading and sediment structure. The fixed-effects influence in the model was set as the interaction related to each treatment (four levels) and sampling time (the number of levels depended on parameter and phase: six, eleven and three levels for CR and NEP during colonization, desiccation, and rewetting, respectively; and five and three levels for periphyton during colonization and during desiccation and rewetting, respectively). For the random-effects influence in the response, we allowed different intercepts for each stream in the model. We compared CR, NEP and periphyton of different treatments between experimental phases, running an additional LME without sampling time in a fixed structure of the model. H:A ratio, F:B ratio, and water quality parameters were compared only between the colonization and rewetting phase. Each LME was followed by model validation to check residuals for normal distribution and homogeneity of variances. The statistical significance of relationships was tested using a

likelihood-ratio test by comparing the model with and without the interactions between factors. The LMEs were followed by a conservative Turkey's post-hoc test to examine significant differences between treatments. All statistical analyses were performed in the statistical software R, using the packages lme4, MASS, and lsmeans, at a significance level of $p \leq 0.05$.

3. Results

3.1. Community respiration (CR) and net ecosystem production (NEP)

CR and NEP showed a significant relationship to shading during all phases (Fig. 3, CR: $\chi^2_{col} = 12.08$, $p < 0.001$, $\chi^2_{des} = 5.27$, $p = 0.02$, $\chi^2_{rew} = 4.92$, $p = 0.03$; NEP: $\chi^2_{col} = 4.78$, $p = 0.03$; $\chi^2_{des} = 103.82$, $p < 0.001$; $\chi^2_{rew} = 25.53$, $p < 0.001$), and were strongly affected by drying (pairwise *t*-test, $p < 0.001$) and rewetting ($p < 0.001$). CR decreased more (60%) in high shade streams than in low shade streams (40%) after flow cessation ($p < 0.001$). NEP and CR decreased to near-zero after 20 days' drying. After flow resumption, CR peaked within a few hours and declined thereafter to lower than before drying ($p < 0.0001$). NEP recovered slowly, starting from similar low values in all experimental streams ($p = 0.2$), but reaching higher levels in high shade and similar levels in low shade streams than before desiccation ($p < 0.0001$).

3.2. Periphyton biomass and structure

Periphyton biomass was significantly related to shading in all phases (Fig. 4, $\chi^2_{col} = 32.82$, $p < 0.0001$; $\chi^2_{des} = 23.24$, $p < 0.0001$; $\chi^2_{rew} = 37.11$, $p < 0.0001$). During colonization, algal biomass was doubly high ($p < 0.0001$) in the low shade stream. During the first week of desiccation, total biomass in all streams changed little, but decreased in the subsequent two weeks (high shade: $p = 0.006$, low shade $p = 0.03$). After rewetting, the total periphyton biomass in low shade streams was similar to pre-desiccation levels ($p = 0.61$), but lower in streams with high shade ($p < 0.0001$).

Shading affected all periphyton groups during all experimental phases ($p < 0.0001$) (Fig. 4). Biomass increased within each group ($\chi^2_{cyano} = 32.82$, $p < 0.0001$; $\chi^2_{diatom} = 27.89$, $p < 0.0001$; $\chi^2_{green} = 7.63$, $p = 0.006$) in low shade streams compared to high shade streams (Fig. 4). In streams with more light, desiccation caused a shift among periphyton groups related to sediment structure. During the first days of desiccation, diatoms decreased significantly ($p < 0.0001$) and green algae increased ($p = 0.003$), recovering to stable levels similar to pre-desiccation. However, after the first week of drying, cyanobacteria increased ($p = 0.02$) and green algae decreased ($p = 0.001$), irrespective of sediment structure.

Diatoms were affected by interactions between sediment structure and shading ($\chi^2_{des} = 9.29$, $p = 0.0023$). In mixed sediment, their biomass continued to decrease ($p < 0.0001$) regardless of shading, while in sorted sediments, biomass remained constant during the entire desiccation period. Shading was also a dominant factor after flow resumption. Under low shade conditions, the biomass of all groups steadily increased, and in the case of cyanobacteria and green algae, rose to higher levels than before drying ($p < 0.0001$). However, growth of cyanobacteria and green algae was faster than that of diatoms, which did not return to pre-desiccation biomass levels ($p < 0.0001$), leading to a shift in biomass dominance during recovery towards green algae. Under low light, growth of all groups was considerably reduced, and biomass was much lower than before desiccation. Consequently, the shift among groups was clear and mainly caused by the substantial decrease of diatoms during desiccation.

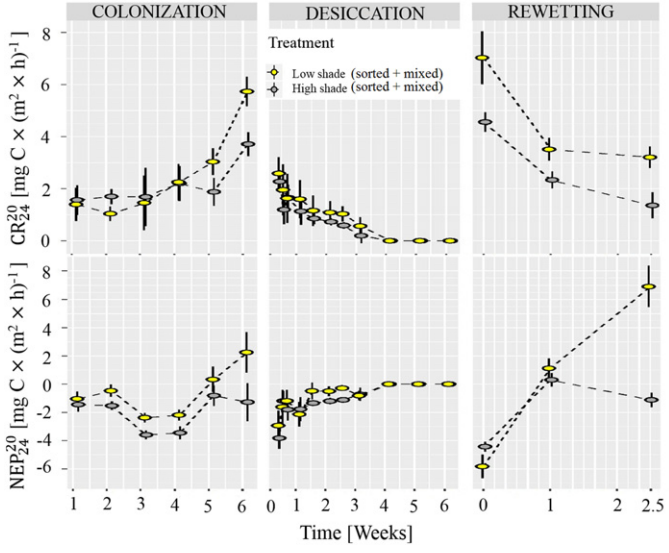

Fig. 3. Dynamics of daily community respiration (CR_{24}^{20}) and daily net ecosystem production rates (NEP_{24}^{20}) for low shade (yellow filled markers) and high shade streams (grey filled markers). Values are means (±SD, n = 8) within each experimental phase (colonization, desiccation, and rewetting).

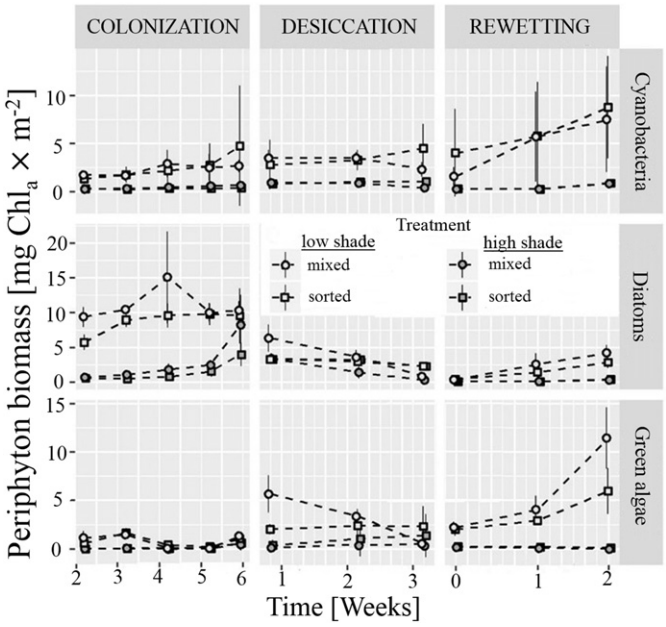

Fig. 4. Dynamics of cyanobacteria, diatom, and green algae biomass for low shade (yellow filled markers) and high shade streams (grey filled markers). Squares and circles represent periphyton biomass in streams with sorted and mixed bed sediment, respectively. Values are means (±SD, n = 4) within each experimental phase (colonization, desiccation, and rewetting).

3.3. Microbial ratios in the benthic community

The heterotroph to algae ratio (H:A) was significantly related to shading (Fig. 5, $\chi^2 = 24.53$, $p < 0.0001$) at the end of the colonization and rewetting phases, and was higher in high shade streams ($p < 0.0001$), regardless of sediment structure. After rewetting, the H:A ratio for both shading treatments was higher than at the end of colonization ($p < 0.001$). The fungi to bacteria ratio was significantly related to sediment structure (Fig. 5, $\chi^2 = 10.82$, $p < 0.01$) at the end of the colonization and rewetting phases, and was lower in sorted streams ($p =$

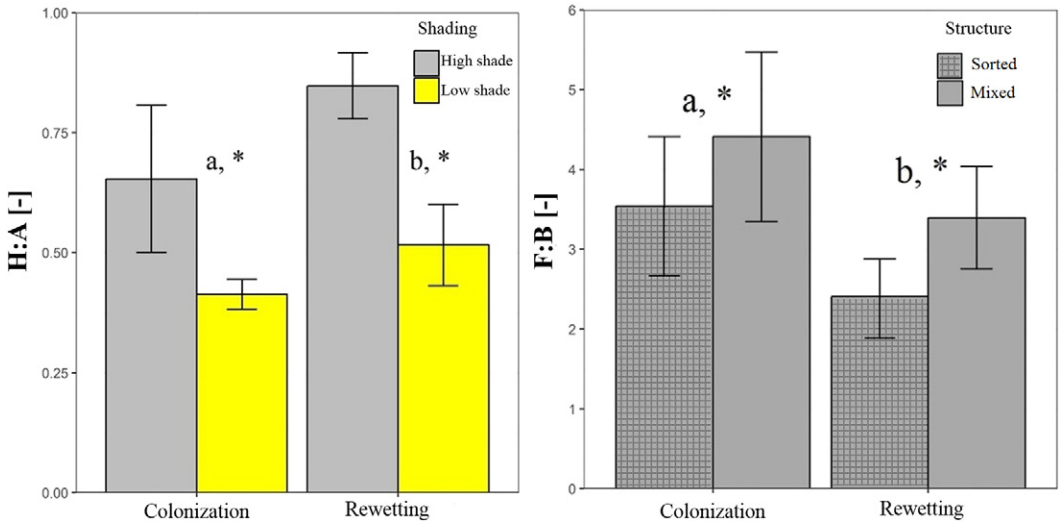

Fig. 5. Ratio of the heterotroph to autotroph biomass (left) for high shade (grey) and low shade streams (yellow), and the fungal to bacterial biomass (right) for sorted (mesh pattern) and mixed bed sediments (grey). Values are means (±SD, n = 8) at the end of the colonization and rewetting phases.

0.01), irrespective of shading level. After rewetting, the F:B ratio was lower in all streams ($p = 0.002$) than at the end of colonization.

3.4. Water quality parameters

Table 1 shows the differences in the main water parameters between treatments. TOC was significantly related to experimental phase ($\chi^2_{phase} = 10.8$, $p < 0.01$), and was higher upon flow resumption than during the colonization and rewetting phases ($p < 0.001$), that were similar. SRP was significantly related to shading ($\chi^2 = 10.8$, $p < 0.01$); high shade streams had higher SRP than low shade streams during colonization and rewetting phases ($p_{col} < 0.001$, $p_{rew} < 0.0001$). SRP upon flow resumption was higher than during the colonization phase in all streams ($p < 0.0001$). DIN was significantly related to shading ($\chi^2 = 36.6$, $p < 0.0001$) and sediment structure ($\chi^2 = 7.1$, $p = 0.03$). Low shade had lower DIN than high shade streams during colonization and rewetting phases ($p_{col} = 0.03$, $p_{rew} < 0.0001$). DIN upon flow resumption was lower in mixed streams than in sorted streams for both shading levels ($p_{low} < 0.001$ and $p_{high} = 0.04$).

3.5. Vertical water flux (VWF) and sediment water content

VWF was higher in streams with sorted sediments, regardless of shading and experimental phase ($p < 0.0001$, Table 1). Water drainage prior to natural desiccation reduced the sediment water content to 72% and 58% of sediment saturation (226.9 mg H_2O g^{-1} DM_{sed}) in mixed and sorted sediments, respectively (Fig. 6). Both sediment structures lost the largest amount of water during the first week (93 and 60 mg H_2O g^{-1} DM_{sed} in mixed and sorted bed sediment, respectively). The differences in water loss between treatments were smaller in the second week (64 and 58 mg H_2O g^{-1} DM_{sed} in mixed and sorted bed sediment, respectively), while differences during the third and following weeks were <3%.

Table 1
Environmental and water quality parameters of experimental treatments. T_{avg} is the mean daily temperature, PAR is photosynthetically active radiation and represents a mean daily value. TOC, DIN, and SRP are total organic carbon, dissolved inorganic nitrogen, and soluble reactive phosphorus in surface water, respectively. VWF is the vertical water flux at the beginning of the colonization phase. Water quality parameters are averages for the colonization and rewetting phase. Flow resumption water quality parameters are for the day of flow resumption. All values are means (±SD, n = 4/n = 8).

Experimental phase	Parameters	Low shade sorted	Low shade mixed	High shade sorted	High shade mixed
Colonization	Tavg [°C]	16.5 ± 0.1		16.3 ± 0.1	
	PAR [μmol/m²/s]	44.2 ± 4.4		26.2 ± 1.0	
	VWF[a] [dm³/m²/h]	4.22 ± 0.92	3.73 ± 0.83	4.22 ± 0.92	3.73 ± 0.83
	TOC [mg C/L]	7.31 ± 0.10	7.41 ± 0.41	8.20 ± 0.21	7.71 ± 0.25
	DIN [mg N/L]	0.20 ± 0.10	0.27 ± 0.04	0.46 ± 0.13	0.48 ± 0.07
	SRP [μg P/L]	9.0 ± 4.8	11.5 ± 4.1	88.8 ± 35.5	87.9 ± 34.5
Desiccation/flow resumption[b]	Tavg [°C]	21.7 ± 0.2		21.4 ± 0.2	
	PAR [μmol/m²/s]	63.0 ± 14.7		34.9 ± 5.1	
	TOC [mg C/L][b]	12.79 ± 2.00	13.71 ± 4.00	9.82 ± 0.46	10.2 ± 1.10
	DIN [mg N/L][b]	0.12 ± 0.03	0.09 ± 0.02	0.25 ± 0.11	0.13 ± 0.03
	SRP [μg P/L][b]	109.9 ± 30.8	125.93 ± 30.49	161.8 ± 42.9	207.95 ± 23.01
Rewetting	Tavg [°C]	16.5 ± 0.0		16.6 ± 0.1	
	PAR [μmol/m²/s]	26.1 ± 5.6		17.0 ± 2.0	
	TOC [mg C/L]	7.58 ± 0.86	7.55 ± 0.32	7.72 ± 0.76	7.84 ± 0.56
	DIN [mg N/L]	0.10 ± 0.04	0.06 ± 0.02	0.68 ± 0.16	0.53 ± 0.17
	SRP [μg P/L]	5.6 ± 2.5	4.2 ± 0.3	136.5 ± 31.6	113.6 ± 12.4

[a] The pore water of the gravel patches in the sorted bed sediments was exchanged within 15 min due to an order of magnitude higher hydraulic conductivity (0.77 cm/s), pore water velocity (2 mm/s) and dispersion (5.75×10^{-4} m²/s) in these patches compared to sand patches. Therefore, in streams with a sorted sediment structure the measured pore water exchange was VWF only in the sand patches.
[b] Values are representative for the flow resumption situation.

4. Discussion

4.1. Effect of light availability on stream metabolism resistance and resilience

We traced stream metabolism changes from periods of low flow to desiccation, subsequent rewetting, and flow resumption, and tested the relationships between the observed dynamics sediment structure, and shading. As expected, streams with low shade became net autotrophic during colonization, while those with high shade remained net heterotrophic. Shade-affected streams were not influenced further by bed sediment structure (Fig. 3), confirming the strong control of light over both NEP and CR prior to disturbance (Wagner et al., 2015). Desiccation can induce changes in the relationships between autotrophic and heterotrophic metabolic processes, causing trophic cascades, and shifting carbon sources and major pathways of energy flow (Power et al., 2008). Just as photosynthetic activity decreases substantially shortly after desiccation (Wyatt et al., 2014), NEP rapidly and sharply declined in our study, shifting stream metabolism to net heterotrophy. The rapid NEP and CR decrease during the first days of desiccation is due to the mortality of benthic communities (Acuna et al., 2004; Castenholz and Garcia-Pichel, 2000), dominated mainly by algal biomass (54% in high shade and 58% in low shade streams). Most drying streams support desiccation-adapted algal communities, like those that remain dormant on dry streambeds until flow resumes, enabling quick reactivation. However, unexpected and rapid drying due to summertime water diversion for agriculture (Barceló and Sabater, 2010) may prevent resistance structures forming (e.g., spores, thickened cells) (Stanley et al., 2004); hence random resistance processes then become important, causing fast, harmful changes to stream metabolism (Holling, 1973; Peterson, 1987).

Progressed desiccation and consequent low moisture content (from 72% and 58% in mixed and sorted streambeds, respectively, after flow recession to <5% after 20 days in all streams) diminishes the ability of microbial communities to use water as a transport and reaction medium. Consequently, nutrients required to sustain microbial metabolism are limited (Schimel et al., 2007), resulting in low and eventually decreasing metabolic rates, observed in both NEP and CR during the desiccation phase (Febria et al., 2012). In parallel, this situation promotes structural and metabolic adaptations to maintain basic ecological functions (Moyano et al., 2013), which are further controlled by environmental factors (light, temperature, water content). We observed that higher NEP and CR rates in desiccated low shade streams were generated by periphyton activity, which shifts to types with lower nutrient requirements only in streams with higher light availability (Fig. 5). Consequently, our study reveals that the sensitivity of periphyton communities and hence metabolic functions to drought is modified by light availability, implying that it is a strong mediator of metabolic resistance to drought stress in canopied streams.

Following flow resumption, CR peaked within a few hours in all experimental streams (Fig. 3). Extracellular enzymes have been reported to resist sediment desiccation (Marxsen et al., 2010; Pohlon et al., 2013), and activity pulses that alleviate microbial processes from moisture limitations after initial rehydration have previously been recognized (Timoner et al., 2014; Baldwin and Mitchell, 2000). Accumulation of organic matter and nutrients in a drying streambed has previously been reported and attributed to biomass senescence and low mineralization rates in the dry sediments (Amalfitano et al., 2008; Humphries and Baldwin, 2003). Rapid mobilization of such readily available organic matter and nutrients from the dry bed sediments is reflected in the elevated TOC and SRP values of the re-established circulating water (Table 1). Microbial cells could rapidly shift out of dormancy (Schimel et al., 2007) using these nutrients, resulting in the initial pulse of CR. CR rates leveled out in the two weeks following rewetting (Fig. 3), suggesting a link between respiration recovery and the growth of communities after the initial pulse (Meisner et al., 2015). Growth of periphyton after rewetting was again positively related to light (Fig. 4), and probably also supported higher CR in lower shade streams (Fig. 3). However, for the 2.5-week rewetting period, CR remained lower than pre-desiccation levels while NEP recovered fast and even exceeded pre-drying levels in low shade streams. This further implies a distinct resilience of photosynthetic and respiration activities after rewetting (Fig. 3), and suggests a shift in community composition with desiccation.

4.2. Effects of light availability and sediment structure on shifts in microbial communities during desiccation and rewetting

Drying can reduce microbial biomass and eliminate species because few are able to resist drying. In our study, streambed desiccation reduced periphyton biomass by 70%, compared to 60–90% of active chlorophyll loss during sediment desiccation in air-dried sediments (Qiu and McComb, 1995). Interactions between shading and sediment structure influenced periphyton biomass structure shifts during desiccation and after rewetting (Fig. 4). In low shade streams, rapid decreases in dominant diatom biomass (Cardinale et al., 2002; Steinman et al., 1992) within the first week of desiccation were accompanied by an increase in green algae biomass, suggesting interspecies competition for nutrients in periphyton communities. In comparison to diatoms, which are more competitive for nutrients during early colonization (Stevenson, 1983), late colonists such as green algae and cyanobacteria have a high affinity for limiting nutrients (Peterson and Grimm, 1992). These features are advantageous when the availability of nutrients for algal cells was limited to capillary diffusion (Haghighi et al., 2013) due to the lack of nutrient transport during flow recession (Fig. 4).

Progressive drying of low shade streams caused further decreases in diatoms related to the sediment structure. While the biomass of diatoms in mixed bed sediments continually decreased, in accordance with the initially higher drying intensity found in these streams (Fig. 6), it remained constant with desiccation in the sorted bed sediments. Capillary water from the shallow hyporheic zone of sand patches serves as a refuge for diatoms seeking wet areas (Minckley and Marsh, 2009) after rapid drying of the gravel patches. Lower DIN and SRP concentrations after rewetting in sorted streams (Table 1) with low shade further imply longer community persistence in sorted bed sediments where autotrophic and heterotrophic communities preserve their activity by consuming these nutrients (Minckley and Marsh, 2009). In drying streams diatoms are generally limited to a few species (Tornés and Ruhí, 2013), whereas the most desiccation-resistant species are primarily green algae and cyanobacteria (McKew et al., 2010). All algal groups' biomass decreased during desiccation in high shade streams, and no community shift was observed (Sabater et al., 2000). The increase of cyanobacteria in low shade streams reflects their better structural adaptation to

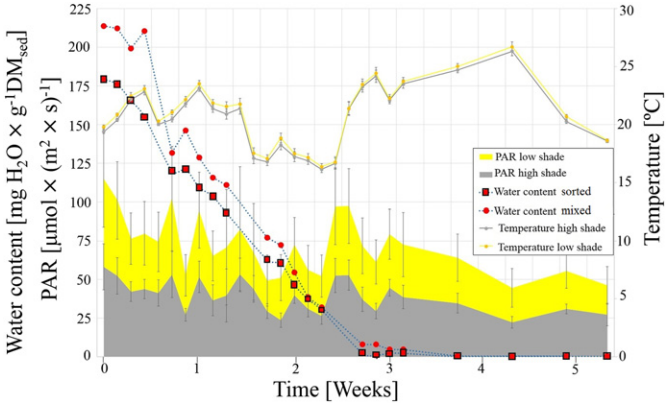

Fig. 6. Water content, sediment temperature, and photosynthetically active radiation (PAR) in the experimental streams during desiccation.

desiccation with higher light availability. The ability of green algae and cyanobacteria to persist with decreasing moisture is positively related to their ability, driven by light availability, to recover their optimum hydric conditions (Timoner et al., 2012). For instance, scytonemin occurs in the extracellular polysaccharide sheaths of cyanobacteria (Garcia-Pichel and Castenholz, 1991), and has been observed in microbial mats (Fernandez-Valiente et al., 2007) and soil crust biofilms exposed to desiccation and high solar radiation (Belnap and Lange, 2001). This pigment helps communities resist desiccation and recover faster after rewetting (Romaní and Sabater, 1997).

The rewetting phase in our study was indeed accompanied by a further increase in cyanobacteria, fast recovery of dormant green algae, and poor recovery of diatoms in low shade streams. Conversely, periphyton biomass remained the same as that during desiccation in high shade streams. The dry phase has lasting effects on communities in subsequent hydrological phases, causing a lagged response in algal diversity and biomass (Datry et al., 2017). The length of these effects is further controlled by light availability after flow resumes. The lower F:B ratio after rewetting in sorted sediments than mixed bed sediments (Fig. 5) indicates the significance of the preceding drying intensity also for heterotrophic recovery (Acuna et al., 2015; Marxsen et al., 2010), which has also been found in other studies (Amalfitano et al., 2008; Chauvet et al., 2016; Tzoraki et al., 2007). While both bacterial and fungal communities seek refuge in the hyporheic zone when surface flow ceases, conditions for fungal development in this habitat are suboptimal. For instance, dissolved oxygen concentrations are low, especially in the longer wet sandy patches of the hyporheic zone without water flow, oxygen demand (Field and Webster, 1983; Medeiros et al., 2009) is high, and hence the biomass and diversity of aquatic hyphomycetes are much lower in the hyporheic zone than in the benthic zone (Bärlocher et al., 2006; Cornut et al., 2010; Sudheep and Sridhar, 2012), therefore making benthic fungi less resistant to desiccation. Consequently, drying conditions favor cyanobacteria and green algae (Ylla et al., 2010), and change the occurrence of fungi and bacteria in biofilms. Moreover, the capacity to establish this resilient transient community during desiccation is strongly related to drying conditions, light availability and sediment structure, and promotes varying resistance to desiccation among transient aquatic species (Lake, 2003).

4.3. Decoupled resilience of stream metabolism as consequence of microbial shifts

Despite microbial shifts in the benthic zone during desiccation and rewetting, stream metabolic functions were highly resilient, and their recovery increased with increased light conditions. However, differing recovery levels of NEP (full recovery) and CR (50% recovery), imply decoupled resilience of metabolic activities after rewetting (Fig. 3). Other studies also show that photosynthetic efficiencies can increase with rewetting (Timoner et al., 2012), and prolonged desiccation can induce shifts in dominance to taxa with a physiological features adapted to desiccation conditions (Minckley and Marsh, 2009) but with different metabolic rates (Steinman and McIntire, 1987). Hence, the dominance of green algae in the rewetting period, which are shown to have higher photosynthetic efficiency ($\approx$0.83) (Büchel and Wilhelm, 1993; Flameling and Kromkamp, 1998; Koblizek et al., 2001), promoted photosynthesis in streams compared to the colonization phase where diatoms dominate (photosynthetic efficiency usually $<$0.75). Although CR was found to recover fully within 10–14 days after desiccation and rewetting in isolated sandy sediments incubated under laboratory conditions (Pohlon et al., 2013), good recovery of periphyton biomass (Fig. 4), together with the increase in H:A and decrease in F:B (Fig. 5) after rewetting, was not accompanied by full CR resilience. The lower F:B ratio at the end of rewetting than during colonization may have decreased leaf mineralization rates (Malik et al., 2016), reflected in poor CR resilience two weeks after rewetting in all streams. Moreover, improved nutrient supply in sorted streams, which promotes stream metabolism (Boulton et al., 1998; Edwards, 1998) likely compensated for higher mineralization rates (Malik et al., 2016) induced by the higher F:B ratio in mixed streams. This compensation generated similar CR resilience between different sediment structures, whose rates of recovery were modulated by periphyton biomass and structure recovery mediated by shading after rewetting. This shows that respiration resilience is linked to the balance of autotrophs' and heterotrophs' biomass and structure which are controlled by light availability and sediment structure in intermittent streams.

4.4. Implications of infrequent droughts for low-land temperate streams

Our experiment was designed to compare the responses of moderate and well-canopied temperate streams with different sediment structure to infrequent droughts. We showed that streams with a naturally sorted bed structure, and streambeds degraded by sand input are functionally similar, and their metabolism under desiccation is strongly controlled by light availability. However, community composition changes during desiccation, which are responsible for the recovery of ecosystem functions after flow resumption, are shaped by variable sediment moisture due to differing evaporation from the two sediment structures. The after rewetting restructured periphyton biomass, increased H:A driven by light availability, decreased F:B ratio linked to sediment structure, and decreased CR, indicate that unpredictable and infrequent droughts in lowland streams may substantially alter microbial resistance and resilience, affecting organic matter mineralization. Photosynthesis recovery limits heterotrophy to the desiccation period and to the first week after flow resumption. The shifted balance of ecosystem processes between desiccation and rewetting however might imply that the biogeochemical changes induced by predicted climate change and increased water withdrawal, light availability and sediment structure of intermittent streams and rivers, underlie ecosystem function resistance and resilience. Given estimates on the increasing number of intermittent streams and rivers, this study have significant benefits for the future management of intermittent streams under a changing climate and land use, particularly for prediction of short and long-term stream responses to infrequent droughts in temperate ecosystems.

Author contributions

All authors contributed equally to this study. All authors have approved the final version of the manuscript.

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